

In both species oocyte maturation is a continuous process that occurs throughout the reproductive period (Tables 1, 2) with multiple spawnings occurring. Depleted ovaries containing mainly Type 1 oocytes were not observed until conclusion of the spawning season. The presence of various groups of developing oocytes as occurs in *G. lineatus* and *S. politus* was termed asynchronism by Yamamoto and Yamazaki (1961) who found this condition common in fishes with long breeding seasons and multiple spawnings.

Another difference (Table 1) was the persistence of small quantities of Types 2 and 3 oocytes in *G. lineatus* after the conclusion of spawning in April which persist throughout summer. It is more typical for remaining vitellogenic oocytes to undergo atresia at the end of the spawning season as occurs in *S. politus* whose inactive ovaries contained only Type 1 oocytes (Table 2) from November to January. These low frequencies of mature summer *G. lineatus* oocytes may suggest spawning continued at a reduced frequency during this period. A more plausible explanation might be that these oocytes will ovulate early in the next spawning season. It thus appears that some early ovulating *G. lineatus* oocytes initiated yolk deposition late in the previous spawning season and remained over summer. It may be energetically advantageous for these yolk filled eggs to remain over summer as opposed to resorbing them.

As *G. lineatus* ranges from Baja California to British Columbia and *S. politus* from Baja California to Oregon (Miller and Lea 1972), my data may be useful for subsequent investigations to determine geographic variation in reproduction for these species.

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STEPHEN R. GOLDBERG

Department of Biology  
Whittier College  
Whittier, CA 90608

#### FOOD OF FIVE SPECIES OF COOCCURRING FLATFISHES ON OREGON'S CONTINENTAL SHELF

The purpose of this paper is to describe and to compare the food of five flatfish species that actually cooccurred at one specific time and place on the central Oregon continental shelf: English sole, *Parophrys vetulus* Girard; rex sole, *Glyptocephalus zachirus* Lockington; rock sole, *Lepidopsetta bilineata* (Ayes); petrale sole, *Eopsetta jordani* (Lockington); and Pacific sanddab, *Citharichthys sordidus* (Girard). These demersal fishes are common along the west coast of North America, their ranges overlapping between southern California and the Gulf of Alaska (Hart 1973). *Parophrys vetulus*, *C. sordidus*, and *L. bilineata* occur mainly on the inner continental shelf. *Eopsetta jordani* is fished commercially on its feeding grounds (73-128 m), and in deep water (311-457 m) where spawning occurs (Forrester 1969). *Glyptocephalus zachirus* has a broad bathymetric range—it is common off Oregon and Washington from 90 to 550 m (Alverson et al. 1964). Off Oregon it was the second most numerous member of a species association ranging from 119 to 199 m, on an average sediment type of 69% sand, 19% silt, and 12% clay (Day and Pearcy 1968). In that same study, *C. sordidus* and *P. vetulus* composed 80.3% of a species association of fishes in shallower water (42-73 m) on a sandy bottom. According to Alverson (1960), *L. bilineata* is common on sandy or gravel bottom. The five flatfish species attain maximum sizes ranging from 410 mm for *C. sordidus* to 700 mm for *E. jordani* (Hart 1973).

Pearcy and Vanderploeg (1973) listed major food items—combined from several locations, seasons, and years—for most of the above species. That

study provided generalized information on food habits, but little insight into possible intra- or interspecific differences in diets resulting from actual interaction among cooccurring fishes. Our study is based on a single collection minimizing temporal and spatial variations associated with sampling. Food items were identified to species whenever possible. Thus, a detailed comparison of food taxa is arrived at with minimal geographic and no seasonal effects.

A trawl haul of 75 min total duration was made beginning at 1345 h Pacific daylight time, on 13 April 1975 with an Atlantic-Western trawl (24-m footrope) from the *Betty-A*, a commercial dragger, at approximately lat. 44°42'N, long. 124°24'W. Depth of water was 95-106 m. The sediment was sand (Byrne and Panshin 1968). Stomachs of fishes were removed and preserved in Formalin<sup>1</sup> at sea (Table 1). Food items were identified and enumerated in laboratories ashore.

TABLE 1.—Fishes captured in an Atlantic-Western trawl on 13 April 1975.

Species	No. caught	Total length range (mm)	No. examined	No. with stomach contents
<i>Citharichthys sordidus</i>	181	90- 377	62	26
<i>Parophrys vetulus</i>	50	230- 450	50	37
<i>Glyptocephalus zachirus</i>	24	240- 360	22	21
<i>Eopsetta jordani</i>	22	240- 510	12	7
<i>Lepidopsetta bilineata</i>	19	247- 474	19	15
<i>Raja binoculata</i>	9	940-1,460	8	6
<i>Raja rhina</i>	2	800- 890	2	1
<i>Raja kincaidii</i>	2	560- 570	2	0
<i>Pleuronichthys verticalis</i>	2	251- 254	2	1
<i>Ophiodon elongatus</i>	1	850	1	0
<i>Squalus acanthias</i>	1	1,000	0	—

#### Forage Organisms

All the food items identified from five species of flatfishes are listed in Table 2, and the major food taxa (taxa having a frequency of occurrence of 10% or more) are listed for individual fish of three species of flounders in Table 3.

*Parophrys vetulus* had a diverse diet, feeding primarily on polychaetes and amphipods. Mollusks, ophiuroids, and crustacea were also represented. The amphipod *Ampelisca macrocephala*, the most numerous single prey species, occurred in 60% of fish. The diversity of the diet of *P. vetulus* is

due to the many different types of food consumed by individual fish (represented by the vertical columns in Table 3) rather than by different fish feeding on different prey. *Parophrys vetulus* appears to be an opportunistic feeder. Forrester (1969) reported polychaetes, clams, and ophiuroids as primary food organisms of *P. vetulus*, with incidental occurrences of sandlance, crab, amphipods, shrimp, squid, and small fish. Percy and Vanderploeg (1973) found polychaetes, amphipods, and pelecypods were important prey of *P. vetulus* off Oregon.

*Glyptocephalus zachirus* fed primarily on four species of amphipods and secondarily on polychaetes. Amphipods occurred in all but one stomach, polychaetes in 71% of the stomachs with food. Nematodes were encountered in 38% of the stomachs but were probably parasitic (Robert Olson, pers. commun.). Percy and Vanderploeg (1973) also found polychaetes and amphipods to be the major food of *G. zachirus* off Oregon.

The principal food of *Lepidopsetta bilineata* was ophiuroids. All but one individual had been feeding on *Ophiura*, which constituted the bulk of the stomach contents. A few polychaetes and mollusks were also present. According to Shubnikov and Lisovenko (1964), the basic items of its diet are polychaetes, mollusks, shrimps, and other crustaceans. Fishes (sandlance) and echinoderms were occasionally found in stomachs. Food items reported for *L. bilineata* in Hecate Strait, British Columbia, by Forrester and Thomson (1969) were clams, polychaetes, crabs, shrimps, sandlance, herring, echinoderms, and amphipods.

*Eopsetta jordani* preyed on fishes and decapod crustaceans. Polychaetes and amphipods were not present in its diet. Ketchen and Forrester (1966) found euphausiids, herring, sandlance, and shrimp as major food items in stomachs of *E. jordani*. Percy and Vanderploeg (1973) reported shrimps, pelagic fishes, and euphausiids as major food items, indicating that this species feeds largely on pelagic prey.

*Citharichthys sordidus* had been feeding intensively on the northern anchovy, *Engraulis mordax*. Anchovy were noted in nearly all the sanddab when stomachs were removed, and all intact preserved stomachs contained them. Since anchovy were not caught in the otter trawl, feeding in the net is thought to be unlikely. According to Percy and Vanderploeg (1973), euphausiids, shrimps, amphipods, and crab larvae were common in *C. sordidus* stomachs.

<sup>1</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Taxa identified from stomach contents of five species of Pacific Northwest flatfishes.<sup>1</sup>

Taxa	<i>Parophrys vetulus</i>	<i>Glyptocephalus zachirus</i>	<i>Lepidopsetta bilineata</i>	<i>Eopsetta jordani</i>	<i>Citharichthys sordidus</i>
POLYCHAETA	94.6	71.4	40.0		
Aphroditidae					
<i>Aphrodita negligens</i>			x		
Capitellidae					
[Capitellidae spp.	10.8				
<i>Notomastus</i> spp.	x				
Chaetopteridae spp.	x				
Cirratulidae					
[Cirratulidae spp.	40.5				
<i>Chaetozone setosa</i>	x				
<i>Chaetozone</i> spp.	x				
<i>Tharyx</i> spp.	x				
Goniadidae					
Goniadidae spp.	x	x			
<i>Glycinde picta</i> (?)	13.5				
Lumbrineriidae					
<i>Lumbrineris</i> spp.	18.9				
Magelonidae					
<i>Magelona</i> spp.	x				
Maldanidae spp.	x				
Nephtyidae					
[ <i>Nephtys caecoides</i>	x				
<i>Nephtys</i> spp.	43.2				
Onuphidae					
<i>Nothria geophiliformis</i> (?)	x				
<i>Nothria iridescens</i> (?)	10.8	14.3	13.3		
<i>Nothria</i> spp.		19.0			
Opheliidae					
Opheliidae spp.		9.5			
<i>Ammotrypane aulogaster</i>	8.1				
Orbiniidae					
<i>Haploscoloplos</i> spp.	x				
Oweniidae					
<i>Myriochele oculata</i>	16.2				
<i>Myriochele</i> spp.	10.8				
<i>Owenia</i> spp.	16.2				
Paraonidae spp.	21.6				
Pectinariidae					
<i>Pectinaria</i> spp.	x	x	x		
Phyllodocidae					
<i>Eteone longa</i>	x				
Polynoidae spp.					
Polynoidae spp.			13.3		
Sigalionidae					
[Sigalionidae spp.	18.9				
<i>Thalenessa spinosa</i>	x				
Spionidae spp.	18.9				
Terebellidae					
[Terebellidae spp.	35.1				
<i>Polycirrus</i> spp.	x				
Unidentified	x	x			
GASTROPODA	13.5				
<i>Cylichna attonsa</i>	10.8				11.1
<i>Mitrella gouldii</i>	x				
<i>Mitrella</i> spp. (?)					11.1
PELECYPODA	27.0	9.5	13.3		
<i>Acila castrensis</i>		x			
<i>Axlinopsida serricata</i>	x				
<i>Cardiomya oldroydi</i>	x				
<i>Nucula tenuis</i>	16.2				
<i>Macoma</i> spp.	x				
<i>Tellina carpenteri</i> (?)	8.1		13.3		
Unidentified	x				
SCAPHOPODA	16.2	4.8			
<i>Dentalium</i> sp.	13.5				
Unidentified fragment	x				
Scaphopoda(?)		x			
CEPHALOPODA					
Octopoda					11.1
Beak of <i>Lolligo</i> spp. (?)					11.1
CRUSTACEA	91.9	100.0	6.7	28.6	33.3
Cypris larvae (?)	x				
Copepoda (calanoid)	10.8				
Mysidacea					
<i>Neomysis</i> spp.					11.1
Unidentified				14.3	
Ostracoda (?)	x				
Cumacea	10.8				
Tanaidacea	x				

TABLE 2.—Continued.

Taxa	<i>Parophrys vetulus</i>	<i>Glyptocephalus zachirus</i>	<i>Lepidopsetta bilineata</i>	<i>Eopsetta jordani</i>	<i>Citharichthys sordidus</i>
Euphausiacea					
<i>Euphausia pacifica</i>					22.2
Decapoda					
Natantia					
<i>Crangon</i> spp.					11.1
Nectocrangon spp.				14.3	
Unidentified shrimp					x
Reptantia					
<i>Pagurus samuelis</i>			x		
<i>Mursia</i> spp.				14.3	
Crab leg		x			
Amphipoda	83.8	95.2			
Ampeliscidae					
<i>Ampelisca cristata</i>		x			
<i>Ampelisca macrocephala</i>	59.5	33.3			
<i>Ampelisca</i> spp.	x				
Amphilochidae spp. (?)	x				
Aoridae					
<i>Lembos</i> spp.	x				
Argissidae					
<i>Argissa hamatipes</i>	x				
Isaeidae					
<i>Photis brevipes</i>	x	x			
<i>Protomedeia</i> spp.	x				
Lysianassidae					
Lysianassidae spp.	x				
<i>Acidostoma</i> spp.		x			
<i>Anonyx anivae</i>	x				
<i>Hipomedon wecomus</i>	18.9	28.6			
Oedicerotidae					
<i>Monoculodes emarginatus</i>	x				
<i>Monoculodes</i> sp. #1	x	x			
<i>Synchelidium shoemakeri</i>	x	x			
<i>Westwoodilla caecula</i>	x				
Phoxocephalidae					
<i>Paraphoxus abronius</i>	x				
<i>Paraphoxus daboius</i> (?)	x				
<i>Paraphoxus epistomus</i> (?)	21.6	33.3			
<i>Paraphoxus fatigans</i>	10.8	4.8			
<i>Paraphoxus lucubrans</i>	x				
<i>Paraphoxus milleri</i>		x			
<i>Paraphoxus obtusidens</i>	16.2	33.3			
<i>Paraphoxus variatus</i>	x				
<i>Paraphoxus</i> spp.	10.8				
Pleustidae					
Pleustidae spp.		x			
<i>Pleusymtes coquilla</i>		x			
OPHIUROIDEA	83.8		93.3		
<i>Amphiodia periercta</i>	10.8				
<i>Amphiodia urtica</i>	10.8				
Amphiuridae spp.	10.8				
<i>Ophiura lutkeni</i>	35.1		73.3		
<i>Ophiura sarsii</i>	x				
<i>Ophiura</i> spp.	8.1		20.0		
PISCES		9.5		100.0	100.0
Agonidae				14.3	
<i>Engraulis mordax</i>				14.3	100.0
<i>Glyptocephalus zachirus</i>				14.3	
<i>Radullinus</i> spp.				14.3	
Unidentified		x		x	
Fish scale	x	x			
NEMERTINEA	13.5				
NEMATODA	x	x			
SIPUNCULIDA	2.7		13.3		
ECHIURIDA		x			
ACANTHOCEPHALA		x			
Miscellaneous					
Gastropod egg case	x				
Egg mass	x				
Lenses					x
Unidentified remains	x	x			

<sup>1</sup>Frequency of occurrence is given as a percentage for food taxa whenever these taxa occur in 10% or greater of any of the five species of fishes. Opheliidae were significant on a weight basis in *G. zachirus*, and were combined with *Ammotrypane aulogaster* for calculation of similarity. An "x" denotes any other occurrence.

<sup>2</sup>Taxa enclosed within brackets were treated as a single group in Table 3.

TABLE 3.—Numbers of food items of major<sup>1</sup> taxa in contents of individual fish stomachs. Each vertical column represents one stomach.

Fish species and taxa	Number of food items															Total no.	
<i>Parophrys vetulus</i>																	
POLYCHAETA:																	
Capitellidae				3											1	1	6
Cirratulidae	1	1		1	3	1	1	1	1	1	11	1			1	3	29
<i>Glycinde picta</i> (?)		1		1	1			1			1						5
<i>Lumbrineris</i> spp.				*	*					2	3		1	*	1		10
<i>Nephtys</i> spp.	1	4		7	3			4		*	* 3		10	1	3	1	47
<i>Nothria iridescens</i> (?)			1		1	2						2					6
<sup>2</sup> [ <i>Myriochele oculata</i>											3	1			1	1	8
<i>Myriochele</i> spp.					*			*	*	*							4
<i>Owenia</i> spp.			1					*	1			2	1		*		7
Paraonidae				2	1		1	1	*			5				1	13
Sigalionidae			1				1	2	1			1					8
Sponidae				1	1			2			2		1	1			9
Terebellidae	*	2	1	1	1	1				1	5	2	4	1	*		23
AMPHIPODA:																	
<i>Ampelisca macrocephala</i>		2	1	1	8	3	2		2	5	2	1	12	7	1	2	64
<i>Hippomedon wecomus</i>								1			1	1	1	2	1	1	8
<i>Paraphoxus epistomus</i> (?)										4	2	1	1	1	2		13
<i>Paraphoxus fatigans</i>	1											1		1			4
<i>Paraphoxus obtusidens</i>				2	1			1		1	1	1					7
<i>Paraphoxus</i> spp. <sup>3</sup>								*	1						*	1	4
GASTROPODA:																	
<i>Cylichna attonsa</i>				1		2					1		1				5
PELECYPODA:																	
<i>Nucula tenuis</i>		1			2						2		4	1			12
SCAPHOPODA:																	
<i>Dentalium</i> sp.				3	1			2			1				1		8
COPEPODA (calanoid)				1	1	1		2									5
CUMACEA																	
		2							1				1				5
OPHIUROIDEA:																	
<sup>2</sup> [ <i>Amphiodia periercta</i>				1					1						1	1	4
<i>Amphiodia urtica</i>								1		1				1		1	4
Amphiuridae					1			1									4
<i>Ophiura lutkeni</i>	2		2	1			3	1	1	2	1		1	1	1	1	18
NEMERTINEA																	
		1						1		*			*	*			5
<i>Glyptocephalus zachirus</i>																	
POLYCHAETA:																	
<i>Nothria iridescens</i> (?)						1				1				2			4
<i>Nothria</i> spp. <sup>3</sup>	*						*			3					1		6
Opheliidae							1			1							2
AMPHIPODA:																	
<i>Ampelisca macrocephala</i>	1									2	1	1		2	2		10
<i>Hippomedon wecomus</i>				1			1			3	1		1				8
<i>Paraphoxus epistomus</i> (?)	1	1								2			2	1	1		9
<i>Paraphoxus obtusidens</i>							1	2	3		2		1		1	3	13
<i>Lepidopsetta bilineata</i>																	
POLYCHAETA:																	
Polynoidae			*							*							2
<i>Nothria iridescens</i> (?)														1	3		4
SIPUNCULIDA (?)																	
										1					1		2
PELECYPODA:																	
<i>Tellina carpenteri</i> (?)										1	1						2
OPHIUROIDEA:																	
<i>Ophiura lutkeni</i>	1				1	2	2	4	5	4	1	1	2	3			26
<i>Ophiura</i> spp. <sup>3</sup>		*	*												*		3

<sup>1</sup>Taxa having a frequency of occurrence of at least 10%.

<sup>2</sup>Taxa within brackets were treated as a single group for calculation of similarity.

<sup>3</sup>Taxa not used to determine similarity.

\*Fragment.

### Discussion

The flatfishes examined in this study comprised two distinct feeding types based on the species composition of prey and the frequency of occurrence of major food items. *Parophrys vetulus*, *G. zachirus*, and *L. bilineata* were benthophagous, feeding on benthic infaunal and epifaunal invertebrates, mainly polychaetes, amphipods, and

ophiuroids. *Eopsetta jordani* and *C. sordidus* were piscivorous and fed more on pelagic animals, consuming mainly fishes in addition to shrimp, mysids, euphausiids, and cephalopods. Fishes did not occur in the stomachs of the benthic invertebrate feeders, except for two fishes found in *G. zachirus*.

Differences were sometimes obvious in the food habits of fishes within each feeding type. The

similarity among the food habits of the three fishes that preyed on benthic invertebrates was calculated using commonly occurring prey (Table 3) and Horn's (1966) measure of niche overlap. The overlap was largest between *P. vetulus* and *G. zachirus* ( $C_{\lambda} = 0.40$ ). This is because both fishes fed on the same species of amphipods and the polychaete *Nothria iridescens*. *Parophrys vetulus* preyed on a very diverse array of invertebrate taxa, while *G. zachirus* appeared to be more selective in its feeding.

The amount of food overlap among the other species pairs was low (0.19 between *P. vetulus* and *L. bilineata* and only 0.03 between *G. zachirus* and *L. bilineata*). These low values are explained by the high occurrence of *Ophiura lutkeni* only in *L. bilineata*. Also, *L. bilineata* fed on members of two scaleworm families, Aphroditidae and Polynoidae, neither of which is represented in the other flatfishes.

The food habits of the flatfishes that we found to be mainly piscivorous were also different. *Eopsetta jordani* preyed on various fishes, including benthic agonids, pleuronectids, and cottids, as well as a benthic shrimp and crab, whereas *C. sordidus* fed almost exclusively on the pelagic *Engraulis mordax*.

Partitioning of the food resources among the five flatfish species is obvious from our data—the different, syntopic species fed upon different organisms. According to MacArthur and Pianka (1966), a more productive environment should lead to a more restricted diet in terms of different species eaten, but in a patchy environment this does not apply to predators that spend most of their time searching. If the bottom occupied by *P. vetulus* is inhabited by patches of invertebrates, then this species might be such a scavenging "generalist" predator. Rae (1969) documented a food interaction similar to the one in this study between the lemon sole, *Microstomus kitt*, and witch, *Glyptocephalus cynoglossus*, off Scotland. The witch, restricted to muddy bottoms, fed on a more restricted fauna than the lemon sole, whose diet included the hard-bottom species typical of its habitat in addition to species from muddy-bottom types.

Differences in time of feeding could also account for differences in the species composition of prey. Diel changes in the habits of prey can serve to increase or decrease their exposure to predators, and hence their availability as food (Hobson 1965;

Jones et al. 1973). More so than the other species, the stomach contents of *G. zachirus* were in a late stage of digestion, suggesting that they had fed a longer time before capture than other species.

The diet of fishes is related not only to their feeding behavior but also to their digestive morphology and mouth structure. The size of the mouth relative to body length correlated with the size of food organisms for bothid flounders in Georgia coastal waters (Stickney et al. 1974). Symmetry of the jaws plays an important role in the mode of feeding, as species with symmetrical jaws generally take free-swimming food, while those with asymmetrical jaws are mainly bottom feeders (Yazdani 1969). Flatfishes that feed on polychaetes and mollusks typically have smaller stomachs, larger intestines, and smaller gill rakers with fewer teeth than flatfishes that feed on other fishes (DeGroot 1971; Tyler 1973). The mouths of *P. vetulus*, *G. zachirus*, and *L. bilineata* are small,<sup>2</sup> the jaws and dentition are better developed on the blind side (i.e., asymmetrical), the teeth are incisorlike (bluntly conical in *L. bilineata*), and the gill rakers are without teeth. These morphological adaptations correlate with the preponderance of benthic invertebrates in their diets. The piscivores, *E. jordani* and *C. sordidus*, on the other hand, have larger mouths,<sup>3</sup> nearly symmetrical jaws with sharp teeth, and long gill rakers with teeth.

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<sup>2</sup>Length of maxillary into head on ocular side is  $4\frac{1}{4}$ - $4\frac{2}{5}$ ,  $4\frac{1}{2}$ - $5\frac{1}{4}$ , and  $3\frac{1}{2}$ - $4\frac{1}{5}$ , respectively (Norman 1934); also see Norman for line drawings depicting the relative mouth size of flatfishes discussed in this paper.

<sup>3</sup>Length of maxillary into head is about  $2\frac{2}{5}$  and  $2\frac{4}{5}$  (nearly 3), respectively (Norman 1934).

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MICHAEL J. KRAVITZ  
WILLIAM G. PEARCY  
M. P. GUIN

*School of Oceanography  
Oregon State University  
Corvallis, OR 97331*

#### AGE DETERMINATION OF A TROPICAL REEF BUTTERFLYFISH UTILIZING DAILY GROWTH RINGS OF OTOLITHS

The recent economic expansion of the aquarium fish industry in Hawaii has raised questions concerning the judicious exploitation of reef resources (Pellegrin 1973; Randall 1973; Reese 1973). However, appropriate management strategies cannot be implemented until sufficient biological data have been gathered, allowing a characterization of exploited populations of fishes. The relative paucity of such information concerning the vast majority of reef species underscores the need for future research.

Studies pertaining to the age and growth of fishes are especially useful in the analysis of exploited stocks. Unfortunately, efforts to age tropical fishes in the past have proved to be largely unsuccessful and/or involve considerable expenditures in time and effort (Pannella 1974). However, the recent studies of Pannella (1971, 1974) have initiated the development of a technique for determining the age of tropical fishes without having to resort to more elaborate approaches such as the Peterson method of ageing. Pannella has provided evidence that many species of both temperate and tropical fishes deposit lamellae on their otoliths with a diel periodicity. These lamellae are visible as rings or circuli after the otolith has been properly prepared. In the absence of annuli, these rings may be used to age fish. A recent investigation by Struhsaker and Uchiyama (1976) using this technique was successful in ageing the Hawaiian